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item (4) vol 4

WTR

6/14/95

Composition of an old-growth Douglas Fir
forest in northwestern California

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Douglas Fir (*Pseudotsuga menziesii*¹) is one of the most important components of the coniferous forests of western North America. In the coast ranges of northern California, *Pseudotsuga menziesii* is ubiquitous at low to moderate elevations where it is a dominant or co-dominant tree in several plant communities. Near the immediate coast, *P. menziesii* is an important member of the moist lowland forests, being associated with Western Redcedar (*Thuja plicata*), Western Hemlock (*Tsuga heterophylla*), Grand Fir (*Abies grandis*), Port-Orford Cedar (*Chamaecyparis lawsoniana*), and Coast Redwood (*Sequoia sempervirens*). Toward the drier, interior portion of the north Coast Ranges, *P. menziesii* dominates a mixed coniferous forest with Sugar Pine (*Pinus lambertiana*), White Fir (*Abies concolor*), Incense Cedar (*Calocedrus decurrens*), along with the broad-leaved sclerophylls Tanbark Oak (*Lithocarpus densiflora*), Madrone (*Arbutus menziesii*) and Golden Chinquapin (*Chrysolepsis chrysophylla*) as associates.

¹ Nomenclature after Munz and Keck (1959), Munz (1968).

Waring and Major (1964), Whittaker (1960) and Waring (1969) noted that *Pseudotsuga menziesii* obtains its greatest importance as a community dominant on the warm, drier end of the moisture continuum in this high rainfall region: however, it is intolerant of high moisture stress (Zavitkovski and Ferrell 1970, Heiner and Lavender 1972).

Little actual data are available which accurately describe the nature of this important vegetation type (Sawyer, Thornburgh and Griffin 1976, Sawyer and Thornburgh 1976). This paper provides a phytosociological description of the composition and structure of an undisturbed old-growth *P. menziesii* stand in northwestern California.

STUDY AREA

Location. Sampling was performed in a virgin stand of *P. menziesii* in the canyon of the South Fork of the Trinity River on the lower slopes of South Fork Mountain, Siskiyou County, California (Figure 1). The study area is a 1380 ha tract of land comprising a major portion of the drainage of Happy Camp Creek in the Trinity National Forest. The site is being designated as the Yolla Bolla research natural area by the U.S. Forest Service.

Slopes within the study area average 30° (range of 20°-50°) and face generally NNW to NNE. Elevations range from 900 meters at river level to 1370 m on the divide separating the drainages of Happy Camp Creek and Rough Gulch.

Geology and Regional Soils. The study area is uniformly underlain by pre-Cretaceous metasedimentary rocks: schistose formations of varying composition outcrop on slopes and in the bed of the Trinity River Canyon in the area. The geology of the study area has been investigated only on a reconnaissance basis (Trask 1950).

Soils of the study area have not been mapped in detail; both soils and geology have been investigated in more detail in neighboring areas. Two dominant soils support *Pseudotsuga menziesii* forests in this region of California; the Hugo and Josephine series (Storie and Weislander 1952).

The Hugo series consists of well drained gravelly loams with a characteristically gravelly sandy clay loam subsoil. Profile depth of the Hugo series approaches 1 meter. Surface horizons are slightly acid; subsurface horizons usually show moderate clay accumulation and are typically strongly acid. The Hugo soils often develop over schist, hard sandstone or shale.

The Josephine soils are well drained loams with clay-loam subsoil. Profile depth averages 1.5 meters with moderately acid surface and subsurface horizons. The Josephine soils typically develop over shale or sandstone, and lack the significant gravel component of the Hugo profile.

Soils of the study area fall within this Hugo-Josephine complex, with light brown to light-gray, loamy surface horizons. Surface soil samples (from selected plots) ranged in acidity from pH 4.5 to 6.1 (cf. Table 5).

Regional Climate. Climatic data have been collected since 1939 at Forest Glen (713 m elevation) 16 km downriver from the study area. The second-growth forest near Forest Glen is very similar in floristic composition to that of the study area, thus the weather records from this station are probably quite comparable to conditions in the study area.

The climate at Forest Glen is characterized by cool, wet winters and dry, warm summers. Mean annual temperature for this station is 11.0°C (S.D. = 1.2°C), with an annual range of mean monthly temperatures of 19.9°C . Summer drought is most intense in the months of August and September (Figure 2). Total water deficit (Thorntwaite 1948) is nearly 300 mm/year, with an August water deficit of 107 mm. Mean annual rainfall at Forest Glenn is 1525 mm (S.D. = 424 mm), with an average of only 3.1 percent of the precipitation falling in the warm months of June thru September.

Snowfall is not uncommon at Forest Glen. The mean annual snowfall is 128 cm, with an average January total of 48 cm. Snow can occur as late as mid-May and as early as late October in average years, but it rarely remains on the ground for extended periods, even in midwinter. Evergreen sclerophylls such as *Chrysolepis*, *Arbutus*, and *Quercus chrysolepis* can suffer extensive crown damage under heavy snow loads.

The Forest Glen station is located mid-way along a climatic gradient extending from the coast to the interior in this region. Coastal California at this latitude is characterized by cool

summers with abundant fog (Azevado and Morgan 1974), high water availability (Major 1967) and low temperature amplitudes. The interior areas of the inner north coast ranges facing the Central Valley are drier, warmer and experience greater summer drought and ranges of both diurnal and annual temperatures. The result is a dramatic vegetation change along this climatic gradient (Waring and Major 1964). The study area is located near the wet end of this climatic gradient, but well inland so that summer drought is not reduced by fog. The study area thus lies in a tension zone between the mesic coastal forests and the xeric woodland vegetation of the interior.

DATA COLLECTION AND ANALYSIS

Relevé and Plot Sampling. Twenty-eight relevés were studied on subjectively chosen sites within the study area using the phytosociological methods of Braun-Blanquet (1964). Homogeneity of the relevés was maximized by visual inspection, and relevé size was determined by minimal-area criteria (Mueller-Dombois and Ellenberg 1974). Cover and abundance were estimated, and values assigned each species according to the Braun-Blanquet scale (cf. Table 1). Community stratification, slope, exposure, pH (water paste 1:1 v/v) and soil profile characteristics were noted for each relevé; water availability was estimated subjectively.

In addition, as part of the relevé study, 18 circular plots established contiguously with selected relevés were sampled for

forest structure and composition. Size of these circular plots was also determined in part by minimal area criteria; plot radius was adjusted in increments of 5 m to coincide with relevé size. Plots thus established ranged in area from 706 m^2 (15 m radius) to 2872 m^2 (30 m radius). The size of each relevé (and corresponding plots) is given in the heading of Table 5. Within the circular plots, the diameter breast height (dbh) was tallied for each tree greater than 1.5 m tall. Trees less than 1.5 m tall were counted in two size classes: seedlings (<3 dm tall) and saplings (3 dm to 1.5 m tall). Sampling occurred between 14 August 1975 and 17 September 1975.

Data Analysis Methods. The cover-floristic composition data collected for each relevé was analyzed by construction of an association table (Table 5). A slightly modified version of the algorithm developed by Ceska and Roemer (1971), that separates groups of species which optimally differentiate corresponding sets of relevés, was employed in construction of the association table. The arrangement of the species-relevé array thus obtained identifies groups of species which are repeatedly found in association under uniform habitat conditions.

The tree composition data collected for each plot was summarized by calculating basal area (m^2/ha), relative dominance, density (stems/ha), relative density, and importance value (relative dominance + relative density) for each species.

The relevé data and summarized plot data were analyzed using the polar ordination method of Bray and Curtis (1957). This method has been widely applied to analysis of vegetation data, especially forest composition (Cottam, Goff and Whittaker 1973, Orłoci 1975). Similarity matrices between all plots or relevés were calculated for several community parameters using the similarity function

$$\frac{2 \sum a(i,j)}{\sum (b_i + c_j)}$$

where: $\sum a$ = the smaller of the pair of quantitative values for a taxon summed for all taxa in common between pairs of plots i, j ; $\sum b$ = sum of all quantitative values for plot i ; $\sum c$ = sum of all quantitative values for plot j . This coefficient was then subtracted from a constant (.9 in this study) to obtain the inter-plot distance for a given pair of plots. A distance matrix for the relevé data was constructed using transformed cover values assigned each taxon equivalent to the values of the Braun-Blanquet rating scale (Table 1): the assigned cover value was then transformed by the $\log_{10} \left(\frac{\text{value} + .1}{.1} \right)$ to reduce the effect of sampling error on the distance function. Distance matrices were generated for all plots based on basal area, relative dominance, density, relative density, importance value; and log transformation (as formulated above) of basal area and density.

Three axes (X, Y and Z) were generated from these matrices. Plots representing end-points for a given axis were selected by

an algorithm which maximized the total amount of interplot distance accounted for by the ordination. All remaining plots were then located along each axis based on their distance from each axis end-point. Axes were orthogonalized (Orloci 1966), and correlation coefficients were determined for each ordination based on the distance for any given pair of plots in the three-dimensional ordination plane and their actual interplot distance.

The moisture availability status of each relevé was calculated using the Vegetation Moisture Index (VMI) developed by Waring and Major (1964). Waring and Major sampled selected stands of vegetation representative of the vegetation types of the coastal *Sequoia sempervirens*-*Pseudotsuga menziesii* region of northwestern California, and derived an empirical equation which could accurately and easily predict moisture availability from species composition. Species can be divided into ecological groups based on their distribution along a moisture gradient, and assigned relative moisture index values. The VMI for a stand of vegetation can then be determined by the average of all the relative index values of all species present. Species in the vegetation under study which were not assigned to ecological moisture groups by Waring and Major were placed in moisture classes based on their observed distribution within the study area. High VMI values indicate high water availability.

RESULTS AND DISCUSSION

The forest within the area studied is a complex four-layered community. *Pseudotsuga menziesii*, *Pinus lambertiana* and occasional *Abies concolor* form an overstory canopy reaching 50-60 m height. Emergent canopy coverage averages about 50% within the region, hence light penetration is high. The largest *P. menziesii* here are commonly 300 cm dbh, and the largest *P. lambertiana* reach 350 cm dbh. *Abies concolor* seldom attains stem diameters greater than 200 cm. The mean basal area for all plots sampled was $36.1 \text{ m}^2/\text{ha}$, with *P. menziesii* comprising 71.1% of this value. The highest basal area measured in the area (plot 284) for *P. menziesii* was $74.5 \text{ m}^2/\text{ha}$, a value which is about half that reported as maximum for this species (Fujimori 1972). *Pinus lambertiana*, *P. ponderosa* and *Abies concolor* are nearly equal in the average proportion of the basal area they contribute to the forest, a value of about 8%.

A second tree stratum composed of *Acer macrophyllum*, *Arbutus menziesii*, *Chrysolepsis chrysophylla*, *Cornus nuttallii*, *Quercus chrysolepis* and *Q. kelloggii* reaches heights of 20-25 m. *Chrysolepsis chrysophylla* is the dominant member of this layer, with many individuals reaching 75 cm dbh.

A shrub layer composed of *Amelanchier pallida*, *Berberis nervosa*, *Corylus cornuta* var. *californica*, *Rosa psilocarpa*, *Rubus parviflorus* and *Toxicodendron diversilobum* is found in scattered, open patches beneath the two layered tree canopy: *Berberis nervosa* is the most common member of this stratum.

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Herbs and low shrubs, including *Adenocaulon bicolor*, *Chimaphila umbellata* var. *occidentalis*, *Disporum hookeri*, *Iris tenuissima*, *Lathyrus polyphyllus*, *Rubus leucodermis*, *Trientalis latifolia*, and *Xerophyllum tenax* form a fourth layer.

Association Table. Seven groups of taxa-relevé combinations were identified by construction of the association table (Table 5).

These ecological-sociological groups are discrete in that they can occur more or less independently within the vegetation. The most diverse relevés had several of these groups (cf. Table 2).

The seven groups identified are here classified into one association and six understory ecological groups, or unions.

These are delineated, as given in Table 5, as follows:

Pseudotsuga menziesii/*Berberis nervosa* association

Silene californica-*Erigeron inornatus angustifolius* union

Iris tenuissima-*Xerophyllum tenax* union

Chrysolepsis chrysophylla-*Chimaphila umbellata occidentalis*
union

Quercus chrysolepis-*Toxicodendron diversilobum* union

Trientalis latifolia-*Lathyrus polyphyllus* union

Vaccinium parvifolium-*Dryopteris dilatata* union

One other association occurs in the study area, but was not extensively sampled: the *Carex senta*/*Peltiphyllum peltatum* association which is confined to the riverbed below the annual flood level (Figure 3). Mesic species, such as *Aralia californica*,

Taxus brevifolia, *Rhamnus purshiana* and *Alnus oregana* occur as riparian elements in this association, and are found as components of the *Vaccinium parvifolium*-*Dryopteris dilatata* union near seepage areas in the forest upslope.

Ordination. Variability in the composition of the vegetation appears to be related to three observable parameters: moisture availability, density of tree reproduction, and fire events. These trends of variation can be detected in both the association table and the results of the polar ordination analysis.

Ordination based on \log_{10} .1 of cover for the 28 relevés sampled (Figure 4) reveals the variation of the vegetation along a complex gradient of moisture availability. The X-axis represents the total gradient of moisture observed in the study area; the axis end-points, relevés 293 and 296, having VMI's of 65.0 and 7.4 respectively. The Y-axis represents a portion of the moisture gradient toward the xeric end; the axis end-points, relevés 295 and 302, having VMI's of 9.1 and 25.9 respectively. The Z-axis also represents the total moisture gradient in the study area; the axis end-points, relevés 279 and 293, having VMI's of 61.8 and 7.4 respectively.

Ordinations of the 18 plots sampled based on basal area, relative dominance, density, relative density and importance value of all trees are shown in Figure 5 (X and Y axes only). The total scatter of points in the X-Y ordination plane is a direct

function of the total variation of the particular vegetation parameter analyzed (cf. Table 3). Vegetation parameters with little interplot variation, such as basal area and relative dominance, produce tight clustering of plots nearest the axis end-point most closely resembling the typical condition of that parameter. Density, relative density and importance value show less clustering, and hence more variation (cf. Table 4). Log transformations of basal area, density and importance value prior to calculation of distance matrices failed to improve ordination results (Table 3) and are not reported here. Ordinations for the eighteen tree plots sampled which show tight clustering or scatter can be interpreted by looking at the characteristics of the axis end-points.

Plots 293 and 278, end points for the X-axis in Figure 5A (basal area ordination) represent the opposite ends of a gradient in the importance of *Pseudotsuga menziesii* in the study area. Plot 293, situated on a dry, exposed ridgecrest, exhibits low total basal area for all trees, whereas plot 278 represents the maximum *P. menziesii* basal area encountered. Plots 289 and 276, end-points for the Y-axis, reflect a continuum in the dominance of *Pinus ponderosa* in the region; Plot 276 being nearly totally occupied by this species.

Figure 5B (relative dominance ordination) illustrates well the overall compositional characteristics of the mature tree stratum. As can be seen, there is tight clustering in both the

X and Y axes around Plot 298: Total plot basal area, basal area of *P. menziesii*, *Abies concolor* and *Chrysolepsis chrysophylla* of this plot being nearly equivalent to the respective mean values shown in Table 4 for all plots.

Figure 5C (density ordination) shows the typical tree density characteristics of the study area. End-points for the X-Y axis, plots 289, 276 and 295, have the following characteristics: plot 289, low *Pseudotsuga menziesii* density, and moderate density of *Abies concolor* and *Chrysolepsis chrysophylla*; plot 276, extremely high density of *P. menziesii*, mainly in younger age classes; plot 295, low density for all tree species, being located on a dry, rocky site. Figure 5D (relative density ordination) shows a scatter of plots in the X-Y ordination plane similar to the pattern of variation depicted by Figure 5C.

Figure 5E (importance value ordination) reflects the total observed variation in the forest cover of the study site. Plots serving as axis end-points for this ordination have the following salient features: plot 295, dry rocky, exposed site, low total tree basal area and low total density of reproduction; plot 298, moderate *P. menziesii* basal area, high density of *P. menziesii* reproduction; plot 289, moderate *P. menziesii* basal area and density of reproduction, high relative dominance of *Chrysolepsis chrysophylla*, high *Abies concolor* density; plot 290, high *Pinus lambertiana* relative dominance, high *C. chrysophylla* relative dominance, moderate density of all tree species.

Cover diversity of the relevés sampled increases with inferred moisture availability ($r = .56$; $p > .95$; Figure 6). This relationship holds except where excessive reproduction of saplings and pole-sized *P. menziesii* and *A. concolor* shade and eliminate understory unions. Diversity is also reflected in the number of ecological groups (unions) per relevé (Table 2).

Both *Pseudotsuga menziesii* and *Abies concolor* show a high percentage of individuals in young age classes, indicating they may increase in importance within the forest canopy. Fire undoubtedly played an important role in stand composition under pristine conditions. Abundant evidence of past fire incidence was observed in the study area: most large individuals of *Pinus ponderosa*, *P. lambertiana*, *Calocedrus decurrens* and occasional *Pseudotsuga menziesii* had fire-scars which indicated repeated burning. Fire has not occurred in the area during historic times, and as a consequence a pulse of reproduction has become established. With time, canopy closure on presently open sites with park-like forest cover (cf. relevés 287, 296 and 276, Table 5) will occur, and species favored by more open conditions, such as *Pinus ponderosa* and *P. lambertiana*, will decrease in prominence.

ACKNOWLEDGEMENTS

Robert Robichaux, M. G. Barbour and J. Major are thanked for their critical review of the manuscript.

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Table 1.

The Braun-Blanquet cover rating system and log-transformed cover values generated for use in polar ordination of the relevé data collected in the study (cf. Table 6).

Estimated Cover (%)	Cover Value	log-transformed cover for ordination
>75	5	2.9
50-75	4	2.7
25-50	3	2.4
5-25	2	1.7
1-5	1	1.1
.1-1	+	.3
<.1	R	.01

Table 2.

Cover Diversity (H') of all relevés sampled. H' (DeJong 1975) was calculated using conversion values generated from the Braun-Blanquet cover classes estimated for each relevé (cf. Table 1). The number of ecological groups present in each relevé is also given. An ecological group was considered present in a given relevé if 33% of the species of that group were present.

Relevé	H'	No. of Ecological groups
276	.337	1
293	.208	2
295	.174	2
287	.316	3
280	.325	3
290	.472	3
283	.486	3
275	.363	3
298	.316	3
282	.464	3
302	.483	4
274	.486	4
294	.209	3
299	.626	3

Table 2 continued

289	.474	3
278	.573	2
285	.232	2
300	.560	3
286	.670	2
284	.297	2
277	.262	2
288	.854	2
296	.663	2
279	.626	3
281	.616	1
292	.640	1
301	.662	1
303	.445	2

Table 3.

Summary of vegetation variables ordinated and their respective ordination criteria (r = correlation coefficient, actual interplot distance vs. ordination interplot distance; Σ SID = sum of squared interplot distance for all pair-wise comparisons; % = percentage of total squared interplot distance accounted for).

Vegetation variable	r	Σ SID	% X-axis Y-axis Z-axis		
			X-axis	Y-axis	Z-axis
\log_{10} .1 Importance Value	.86	20.8	57.6	37.9	22.1
\log_{10} .1 Basal Area	.84	22.0	34.0	42.2	22.7
\log_{10} .1 Density	.86	23.8	55.4	35.7	23.1
Basal Area	.95	33.1	47.1	27.4	14.5
Relative Dominance	.94	17.9	72.6	11.1	18.4
Density	.86	43.5	38.6	30.3	17.2
Relative Density	.95	28.5	65.6	23.1	14.3
\log_{10} .1 cover (relevés)	.91	9.5	35.7	27.3	23.1

Table 4.

Summary of and variation in basal area and density for trees in the eighteen plots sampled. Basal area values are in m^2/ha ; density values are in stems/ha.

TAXON	BASAL AREA		DENSITY	
	\bar{X}	Coef. Var. (%)	\bar{X}	Coef. Var. (%)
<i>Psueodtsuga menziesii</i>	25.72	78.4	297.6	123.8
<i>Pinus lambertiana</i>	2.9	199.1	13.4	133.5
<i>Pinus ponderosa</i>	2.5	354.0	5.9	272.8
<i>Abies concolor</i>	2.2	330.0	81.5	142.0
<i>Arbutus menziesii</i>	1.1	117.1	23.0	143.0
<i>Chrysolepsis chrysophylla</i>	1.0	157.1	29.4	119.7
<i>Quercus kelloggii</i>	0.9	251.3	18.0	221.6
<i>Calocedrus decurrens</i>	0.5	209.5	9.2	182.6
<i>Quercus chrysolepis</i>	0.1	250.0	2.6	203.8
<i>Cornus nuttallii</i>	0.1	400.2	10.1	305.9
<i>Acer macrophyllum</i>	0.1	300.0	1.3	307.6
TOTALS	36.17	70.5	474.6	82.3

Table 5. Association table depicting the phytosociological groups identified in the study. Roman Numerals to the left of each taxon are the Vegetation Moisture Index classes assigned by Waring and Major (1964), except those indicated by an asterisk, which were given class ratings by the author.

[illegible]

Legends for Figures 1-6

Figure 1. Map of a portion of the Trinity National Forest, Siskiyou County, California. The study area is outlined at lower right.

Figure 2. Seasonal course of water availability plotted for Forest Glen, Siskiyou County, California. Potential evapotranspiration, water deficit (WD), and soil storage (SS) were calculated using the method of Thornthwaite (1948) as modified by Black (1966).

Figure 3. Photograph of the South Fork of the Trinity River in the study area. The Carex senta/Peltiphyllum peltatum association is confined to the river-bed below the level of the mean annual high water mark. Large shrubs below the level of highest floods are Alnus oregana and Rhamnus purshiana. Pseudotsuga menziesii dominates the forest above the highest level of flooding. 15 August 1975.

Figure 4. Plot of ordination of the 28 relevés sampled in the study: axis end-points for the X-axis are indicated by solid triangles; axis end-points for the Y-axis are indicated by solid squares; axis end-points for the Z-axis are indicated by solid circles; open circles indicated the ordinated location of individual relevés. 4A: X-Y axes. 4B: Y-Z axes. 4C: X-Z axes.

Legends for Figures 1-6 concluded.

Figure 5. Plots of ordinations of the eighteen plots sampled (X-Y axes only) based on selected vegetation parameters: axis end-points for the X-axis are indicated by solid triangles; axis end-points for the Y-axis are indicated by solid squares; axis end-points for the Z-axis are indicated by solid circles. 5A: Basal Area ordination. 5B: Relative Dominance ordination. 5C: Density ordination. 5D: Relative Density ordination. 5E: Importance Value (Relative Dominance + Relative Density) ordination

Figure 6. Scatter of cover diversity (H') against Vegetation Moisture Index (V.M.I.). H' was calculated using the minimum cover class values (cf. Table 1) from cover estimates for each relevé by taking the \log_{10} of the value as discussed in the text. V.M.I. was calculated for each relevé using Waring and Major (1964). Correlation coefficient (r) = .56; significant at the 5% level.

Figure 2 (Xerox)

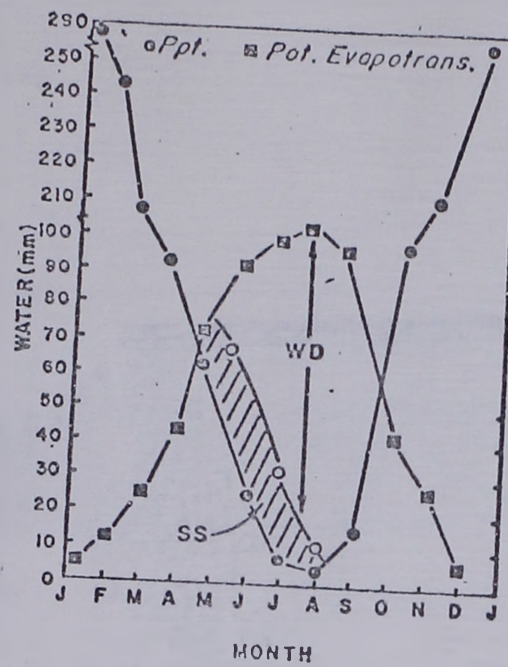


Figure 3.

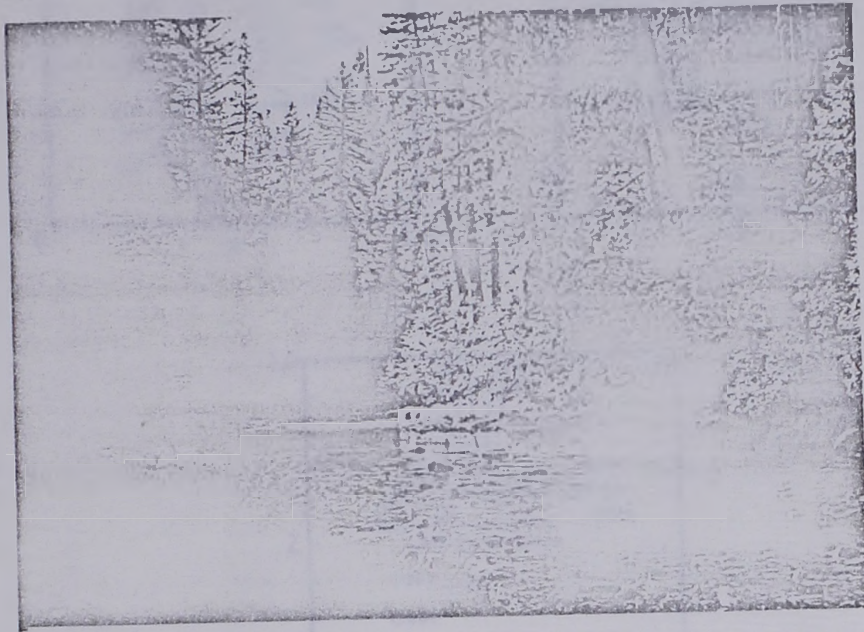


Figure 4 (Xerox)

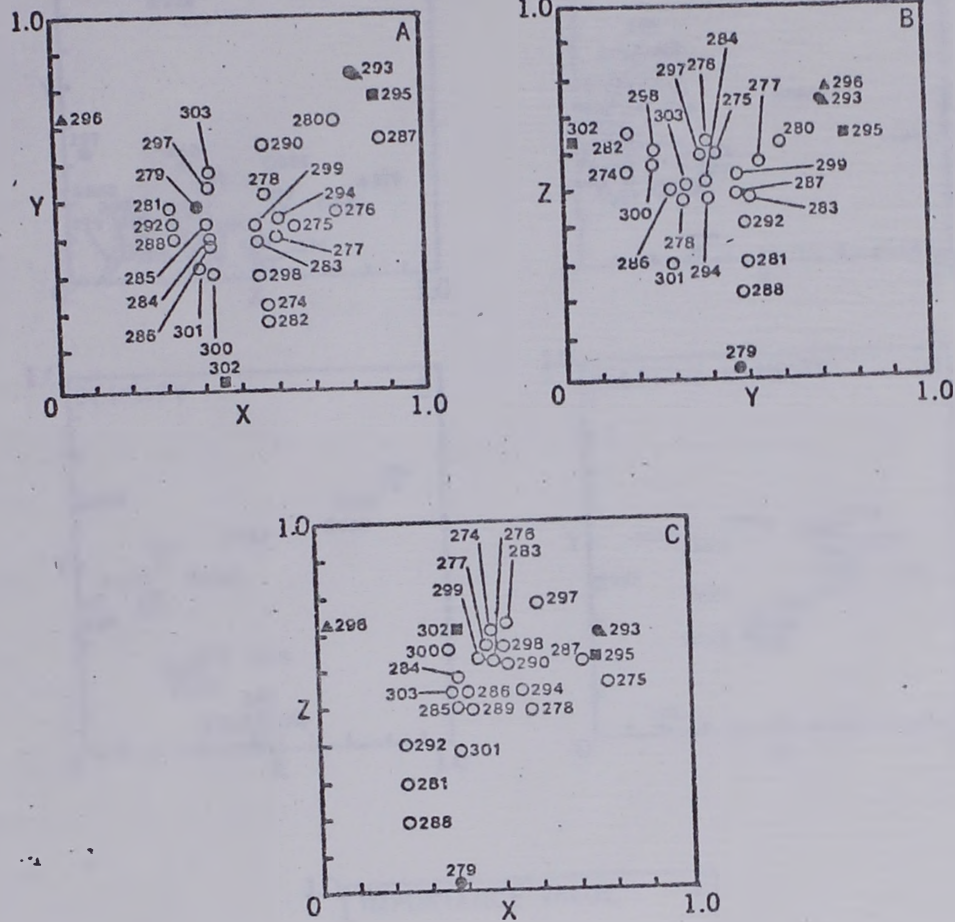


Figure 5 (Xerox)

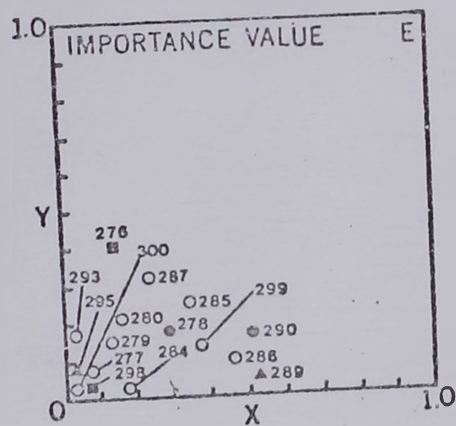
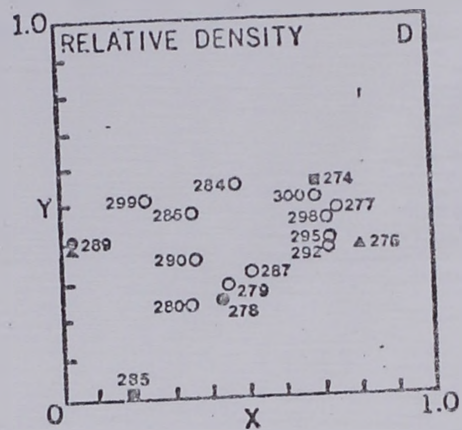
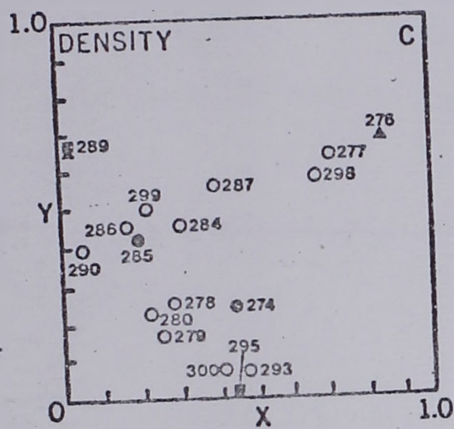
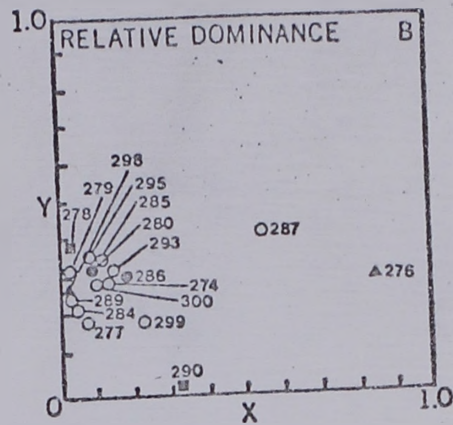
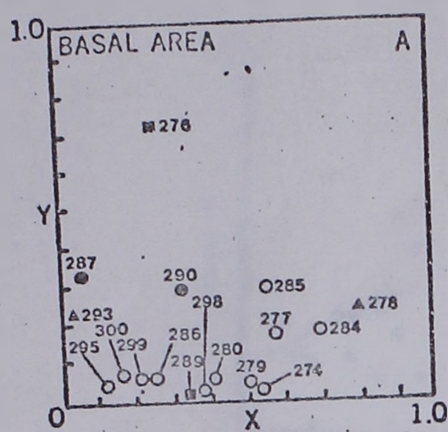


Figure 6 (Xerox)

